

A REVIEW OF THE PHYTOGEOGRAPHIC EVIDENCES FOR PLEISTOCENE CLIMATE CHANGES IN THE NEOTROPICS¹

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ABSTRACT

A review is given of the various botanical evidences for changes in vegetation cover of the Neotropics during the Pleistocene dry periods. Authors who have discussed vegetation changes in terms of plant geography are treated. There are considerable phytogeographic data which support the findings of palynology and geomorphology. The climate changes appear to have affected the vegetation of the entire neotropical region since evidence is presented from Mexico to Southern Brazil and from both the lowland and highland regions. The comparatively recent recognition of climatic and related vegetational changes have caused botanists to re-evaluate some of their earlier theories of speciation and biological diversity in the lowland tropics.

INTRODUCTION

The refuge theory proposes large changes in the vegetation cover and plant species distributions of the lowland tropics during the Pleistocene and Holocene. The theory was developed in the Americas by a zoologist (Haffer, 1969) and since then many other zoologists have also furnished zoogeographic evidence. Considering the implications of the refuge theory for botany there have been few papers about refugia by botanists based on plant distributions and vegetation types. Consequently there is a relatively small literature base about plants and refugia. However, the changes in plant distribution and vegetation types are obviously basic to the refuge theory. The lack of botanical papers about refugia is partially due to the inadequate specimen sample from the region. Only two botanists have proposed locations of refugia over an extended area. The highland areas of South America have been studied in some detail (B. Simpson, 1975, 1978). The lowland refugia of Haffer (1969) were discussed and modified slightly in light of plant distributions by Prance (1973, 1981a). There are, however, several discussions of refugia for smaller areas such as Mexico and adjacent Central America by Toledo (1976), Chocó in Colombia by Gentry (1981), and Venezuela by Steyermark (1979, 1981).

Until recently botanists explained plant speciation in the lowland tropical rain forests under the assumption that the forest had remained stable over a long period of geological time (e.g., Federov, 1966; Ashton, 1969; Richards, 1969). Only recently have botanists come to recognize that this presumed stability of the forest was not necessarily the case, and that quite recent changes in climate

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must be considered as an important factor in plant geography, in speciation, and as a cause of extinctions.

The new emphasis on the instability of the rain forest vegetation in the Pleistocene and post-Pleistocene period does not necessarily eliminate the importance of some of the other models of plant speciation. For example, in the Amazonian rain forest habitat there are an enormous number of niches available and the niche speciation emphasized by Richards (1969) and Ashton (1969) is likely to be important for the speciation of forest trees and vines. The competition and interaction with pollinators has led to phenological separation, there is separation of closely related species into different strata of the forest, and species pairs with one in the inundated forest and another in the forest on terra firme are common. The danger of discussing any one theory such as refugia is that the other models of speciation will be ignored. However, it now appears that refugia have been one of the most important causes of plant speciation and therefore of species diversity of Amazonia, but the discussion below assumes that other methods of speciation are also important.

Botanical evidence for climate changes in the Pleistocene is based largely on chorological data obtained by mapping plant distributions in order to pinpoint centers of endemism in the lowland forest areas and to indicate patterns of disjunct distribution. Some zoologists have used other techniques. For example, the statistical analysis of geographic variation in lizards (Vanzolini & Williams, 1970) or the genetic analysis of hybrid zones in butterflies (Brown, 1976, 1979; Turner, 1976). Below I have summarized the published botanical evidence for refugia excluding palynology, which has been extensively reviewed elsewhere (e.g., Absy, 1979; van der Hammen, 1974, 1981). Pollen provides the most definite botanical evidence of Pleistocene climate changes in the Neotropics upon which authors have been able to interpret their phytogeographic data. These data are backed up by considerable evidences from geomorphology, for example, by Ab'Sáber (1977), whose map for 18,000 B.P. is shown in Fig. 1. Here I will consider mainly the plant distributional evidences for changes in the vegetation cover of the Neotropics in the Pleistocene. It is now possible to interpret some of the unusual distribution and clusters of endemics because there is a growing quantity of solid evidence from geomorphology and palynology. Much of this is summarized in various papers in Prance (1981b).

ANDEAN REGION

Vuilleumier (1971) was the first botanist to comment on the refuge theory in South America. Her paper was a general review of the geological and palynological evidence for the refuge theory and it also presented considerable details about glaciation in the Andean highlands and the southern tip of South America. The review was based mainly on the speciation patterns of high Andean plant and avian taxa, and the lowlands were not discussed in detail. Although written by a botanist, this paper presented no really new botanical evidences. Attention was drawn to the relationship of the flora of the Venezuelan highlands with that of the plateau of Central Brazil, and to the distribution pattern of the genus *Polylepis* (Rosaceae) in the Andes. The distribution of this genus, which forms

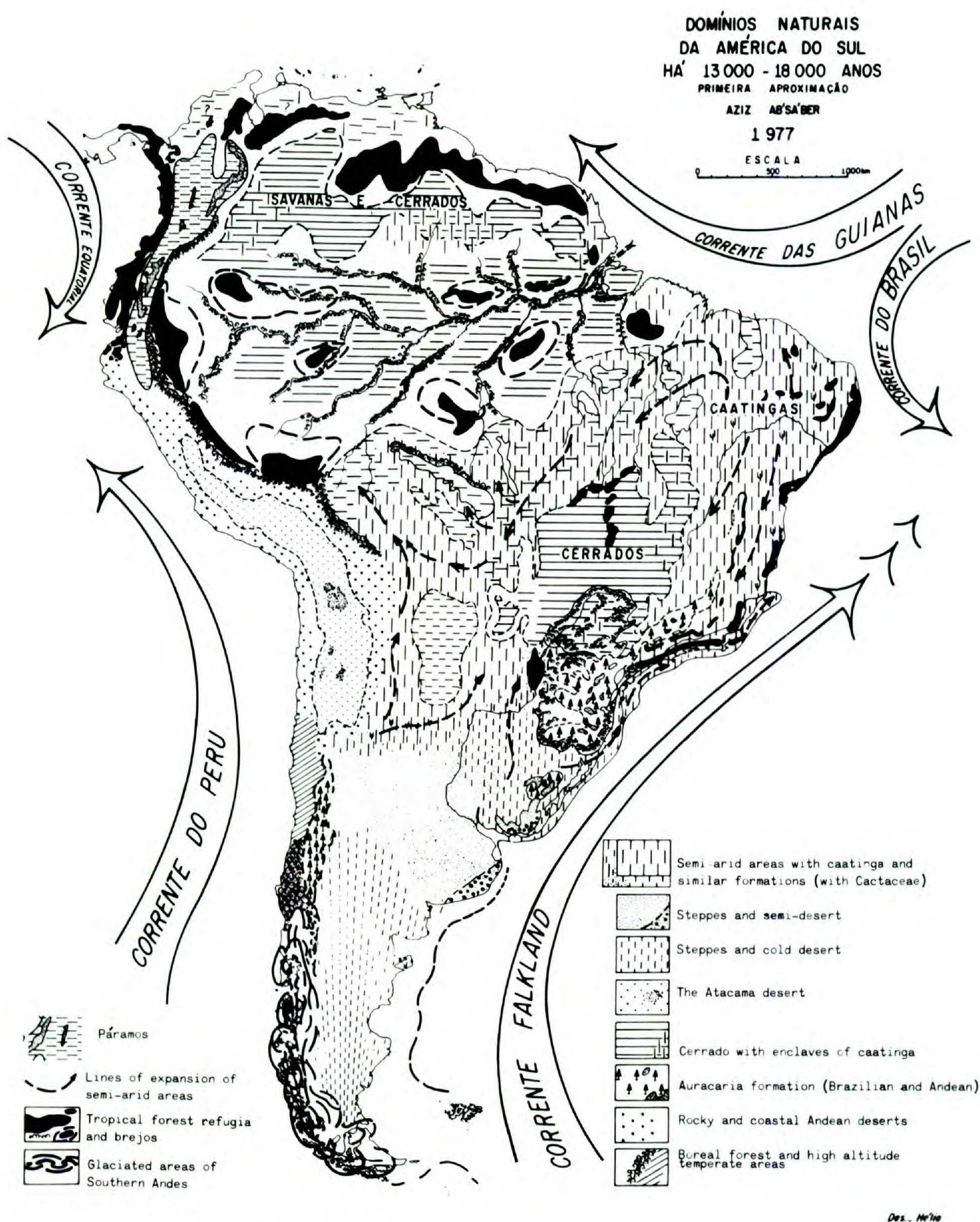


FIGURE 1. The vegetation of South America 13,000–18,000 B.P. as proposed by Ab’Sáber. The black areas are proposed forest refugia, most of the rest of Amazonia is shown as savanna, cerrado, and caatinga, all vegetation types characteristic of drier climate than that of present day Amazonia (from Ab’Sáber, 1977).

distinct isolated patches of woodlands at higher elevations in the Andes, is consistent with a sequence of humid-arid changes in climate along the Central Andean slopes where the tree line changed several times. In a later paper, B. Simpson (1975) presented her botanical evidences in detail. This paper also dealt exclusively with the high tropical Andes, and described the changes during the Pleis-

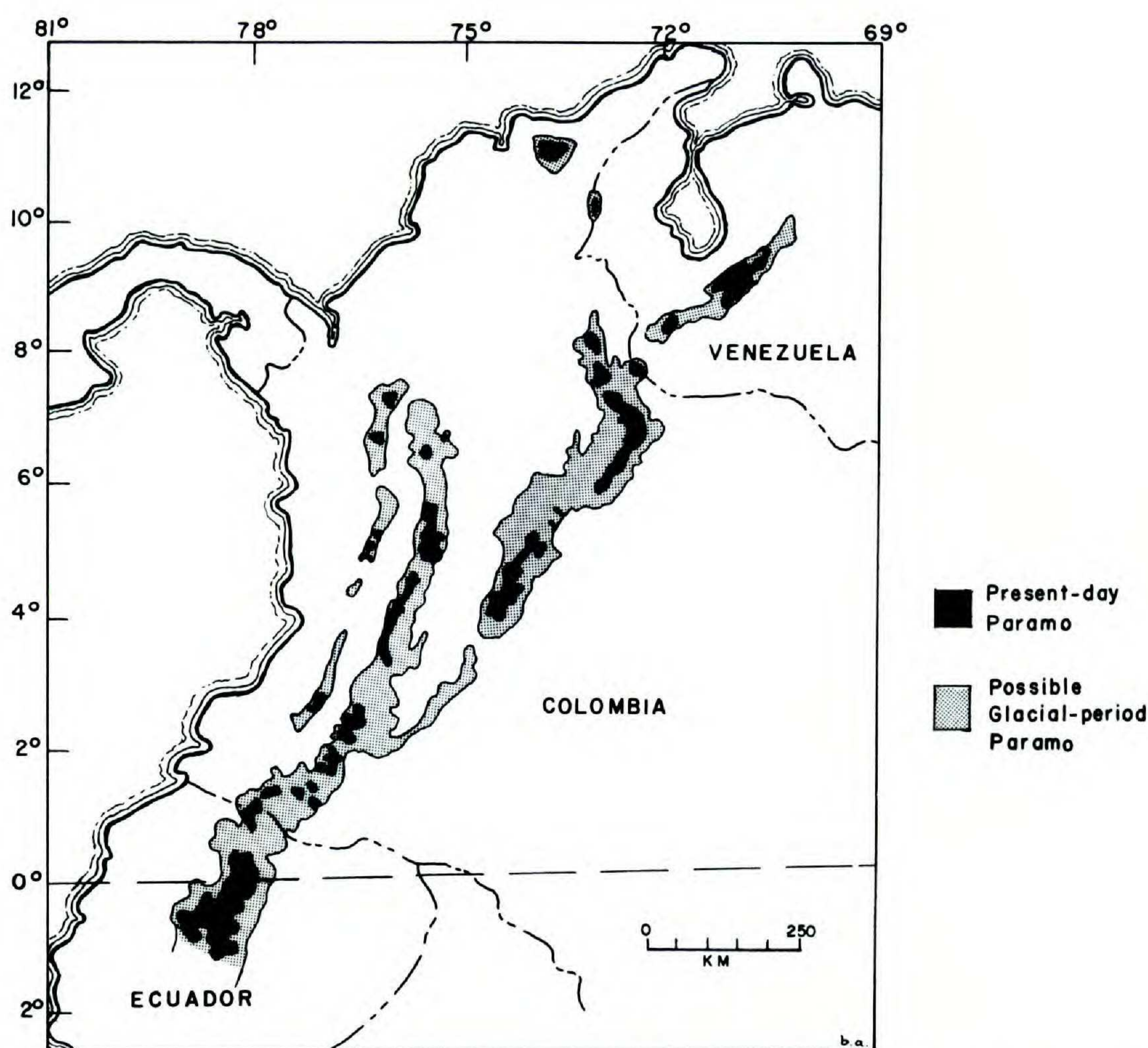


FIGURE 2. The distribution of Páramo vegetation: Present day represented by black areas and Pleistocene maximum glaciation period by gray area, estimated by lowering the altitude by 1,000 m (after van der Hammen, 1981). The black areas also include all areas above the páramo with permanent snow and glaciers.

tocene of the flora at altitudes of over 3,000 m to the páramo of the northern Andes, the puna of the Altiplano, the upper Andean forests, and the dry desert scrub of the high intermontane valleys. Simpson also included a good review of the history of the uplift of the Andes and the gradual availability of the various different Andean habitats for plant colonization. Since most of these habitats have become available primarily in the Quaternary or only the late Tertiary, they are intimately connected with the vegetation of the lowlands. Simpson found an altitudinal and latitudinal variation in the way plant species moved into the Andean habitats, the manner of differentiation during the Pleistocene, and the time of immigration into their habitat. Speciation appears to have taken place mainly through geographic isolation caused by the various changes in vegetation distribution during the Pleistocene and Holocene. With the exception of the Altiplano, most species expanded their ranges when the lowering of the high altitude habitats occurred during the Pleistocene cool periods. For example, in the northern páramos the greatest colonization was during the glacial periods in a manner similar to Oceanic islands. At the lower elevation in the northern Andes of the eastern Cordillera direct migration was possible (Fig. 2). The interglacial periods, which occurred several times, were times of isolation and differentiation. In contrast,

in the Altiplano the glacial periods were times of population fragmentation accompanied by differentiation and/or speciation.

Simpson distinguished two elements in the páramo flora: 1) species groups which are not closely related to lowland groups, and 2) species groups which are closely related to lowland groups. It is the latter that are of interest for the study of the history of the lowland Amazon flora. An analysis of the high Andean flora shows that it was colonized in a way analogous to oceanic islands because there are significant correlations between areas of páramo and their distances from source areas and the number of plant taxa which now inhabit them. There is an even stronger correlation with glacial period parameters and páramo size which suggests that the majority of colonization occurred in glacial periods when plant propagules were able to disperse more easily because of increased size of the páramos.

These highland Andean data together with much palynological work have proved undisputably that there were considerable changes in the highland South American flora during the glacial periods. The changes in páramo in the extreme highlands meant changes in cloud forest and mountain slope forest at lower altitudes. The importance of the slope forest as a possible migration route for plant species must be considered in a discussion of the lowland forest. The details of the lowland flora have not been worked out in such detail as those of the highlands. An interesting part of the highland work is the comparison with and use of some of the concepts of island biogeography which are an integral part of the refuge theory.

FOREST REFUGIA IN THE LOWLANDS

The lowland areas of Amazonia and the refuge theory have been commented upon by various taxonomic botanists from their experience with the groups of plants in which they specialize.

D. R. Simpson (1972), in a paper which was published only in abstract form, studied the distribution patterns of some Amazonian species of Rubiaceae. He observed that these distributions support Haffer's theory for the Peruvian part of Amazonia particularly confirming a floristic difference between the Napo refugium and the east Peruvian refugium further to the south. The most interesting part of Simpson's work was to point out some of the xeromorphic features of trees of the humid forest of Peru. He used these as evidence that xeromorphic traits must have evolved in a xerophytic or subxerophytic climate. He proposed that these species with xeromorphic adaptations are relicts from gallery forests and forest islands which formerly existed in the midst of savannas.

This is an interesting idea. However, there are many present day habitats in Amazonia where xeromorphic adaptations are an advantage such as white sand campinas, black water igapós, and rock outcrops which still offer dry season xerophytic habitats in lowland Amazonia under present day climate conditions. These could also produce xeromorphic adaptations which were retained after the migration of the species into the rain forest. However, such migration is not as likely as that caused by the now well documented climate changes, and subsequent expansion and contraction of forest.

Tryon (1972) discussed centers of endemism and geographic speciation in

tropical American ferns. He pinpointed centers of endemism without any reference to the refuge theory. Centers of endemism are Mexico, the Andes, and southeastern Brazil, with secondary centers in Central America and the Guianas. The intervening, mainly lowland areas are less distinctive in terms of their fern species and tend to have widely disturbed common lowland species. The centers of endemism are important as areas of speciation, species persistence, and as sources of material for migration. Tryon proposed that migration through intervening areas between his centers of endemism occurred both during past climatic changes by continuous dispersal, and by long distance dispersal. He also discussed speciation by isolation after long distance dispersal or loss of continuous distribution.

It is hard to draw any conclusions about lowland tropical areas from this work because ferns thrive at the cooler, higher altitudes and the centers represent this more suitable climate, and also because long distance dispersal is easy for relatively light fern spores. However, it is apparent that the areas of endemism for the ferns must have had stability for a long time and we can look to those areas as a possible source of other plant material for migration into the lowland areas. It is interesting that the lowland ferns do not apparently show regional diversification as a result of the forest refugia; probably this is due to their easy dispersal and relative paucity of fern species in the lowland tropical moist forest.

Langenheim et al. (1973) made an ecological and evolutionary study of the lowland Amazonian species of the Caesalpiniaceous genus *Hymenaea*. They discussed five Amazonian rainforest species together with their relatives in drier habitats and in the Atlantic coastal forest of Brazil. They considered *H. eriogyne* Benth., which occurs in forest islands in the caatingas of northeastern Brazil, and the two species of the Atlantic coastal forests (*H. rubiflora* Ducke and *H. aurea* Lee & Langenh.) as relicts from early Tertiary times when Amazon forest had a more southerly distribution. These species are relicts which have found refugia in eastern Brazil, *H. aurea* in the upland forest of Bahia and *H. eriogyne* in the forest patches within the drier caatinga. Langenheim et al. gave a brief review of evidences for Pleistocene forest changes and accepted them as fact.

Hymenaea shows adaptive radiation from humid rain forest to a variety of drier ecosystem types which they proposed initiated in the mid-Tertiary and continued into the Pleistocene. The authors discussed the habitat and adaptations of each species of the genus. The presence of *H. oblongifolia* Huber var. *palustris* Lee & Langenh. in Chocó, Colombia is said to indicate a more widespread distribution of this species in the past. *H. courbaril* L. var. *subsessilis* occurs on sandy beaches and tributaries of Central Amazonia, and its small tree form is postulated to have developed during the long interval of the Pleistocene. This is not necessarily so because sandy beaches are a present day habitat and one would expect various species to adapt and occupy this niche even without the stimulation of drier periods. The sandy beaches of Central Amazonia have many distinct species or forms of forest species with a smaller stature.

Langenheim et al. stated that "although present evidence regarding speciation within Amazonian *Hymenaea* does not clearly support the hypothesis of dry oscillations during the Pleistocene, it does not negate the possibility." They in-

dicated that there was definite evidence from *Hymenaea* that evolution had responded to dry environmental conditions. *Hymenaea* also demonstrates that the Amazonian hylaea of today is not a vast uniform habitat, but a heterogeneous mixture of seasonally dry forest, savanna, campina, and caatinga, as well as moist forest. The authors questioned the idea of refugia being small peripheral islands as suggested by Vanzolini and Williams mainly because the regeneration of tropical rain forest is slow, and studies demonstrate the slow rate of recolonization of large agricultural areas. These authors felt that the ecology of rain forest trees and their slow invasion of savanna types suggested that relatively large areas of hylaea remained even during the Pleistocene dry climate periods. This is more in agreement with some recent papers on refugia which have tended both to enlarge the area and number of refugia and to emphasize that the area between refugia did not necessarily all become the kind of open savanna we know today, but rather was often an impoverished forest with a reduced species density.

Moore (1973) in a discussion primarily concerned with the worldwide distribution of palm genera, commented briefly on the Pleistocene and recent history of the palms of Africa and South America. He mentioned that the more drastic Pleistocene changes in Africa in comparison with South America were the reason for the depauperate palm flora of Africa (16 genera, 117 species from 7 major groups in Africa compared with 64 genera, 837 species from 9 groups in South America). Moore accepted the data of Haffer (1969) and Vuilleumier (1971) and discussed palms from that assumption. Moore had species data available for only a few palm groups such as *Pholidostachys* and *Geonoma* section *Taenianthera* which seemed to offer a certain amount of support to the refuge theory. This evidence was based on the disjunct distribution of four genera: *Phytelephas*, which occurs in the Panama-Catatumbo refugia and is disjunct in east Peru; *Wettinia* in Chocó and east Peru; *Chelyocarpus* in Chocó and south Peru and Rondonia; and *Orbignya* section *Spirostachys* in Chocó and around Leticia in Amazonian Colombia. From these distributions Moore pointed out the clear relationship between Haffer's east Peruvian and Napo refugia with the Chocó refugia where identical or vicarious species occur. Moore also observed, however, that some species of palms such as the ubiquitous *Mauritia flexuosa* L., *Euterpe precatoria* Mart., *Socratea exorrhiza* (Mart.) Wendl., *Maximilliana martiana* Karst., and *Geonoma deversa* (Poit.) Kunth had been eminently successful either in persisting through change or in redispersing. He also discussed the converse of forest reduction and the present day distribution of some palms of dry areas. The present day distribution of some palms such as some Cocosoid palms, species of *Syagrus* and *Orbignya*, was explained by the fact that the range had been of even greater extent in the past. Moore also reviewed the earlier history and origin of the palms and its possible influence on the more recent history.

I would make two comments on Moore's ideas. Firstly, the evidences he uses for refugia mainly concern the relationship between Chocó and eastern Peru, i.e., a trans-Andean relationship. Undoubtedly, both these areas were stable refugia during the Pleistocene and the palms cited are some of the examples of such a relationship. However, the species were probably isolated earlier by the uplift of the Andes rather than by the Pleistocene climate changes and have not since been

able to coalesce. Chocó is most important as a Pleistocene refugium, but in the case of plants it is much less important as a center of material for redistribution to the other lowlands. Hence, it is a much older and isolated refugium than those which are situated east of the Andes. Secondly, several of the palm species cited above, such as *Mauritia flexuosa* and *Socratea exorrhiza*, are characteristic of wet places such as gallery forests and swamps. They probably persisted with a wide but only slightly reduced distribution during the Pleistocene, surviving in the gallery forests of rivers much as they do today in the gallery of savanna areas.

Prance (1973) studied the distribution patterns of Amazonian Caryocaraceae, Chrysobalanaceae, Dichapetalaceae, and Lecythidaceae, all families of woody angiosperms with their Neotropical distributions centered in Amazonia. This study pinpointed centers of endemism in the lowland forest, discussed morphologically variable widespread species and disjunct distributions such as that of *Stephanopodium* (Dichapetalaceae), which is distributed in northern South America and eastern coastal Brazil. Nineteen maps showed the distribution of several of the species studied. An attempt was made to locate possible refugia and to interpret those of Haffer (1969) in terms of the distribution patterns of forest trees. Prance agreed with the following refugia of Haffer: Chocó, Nechi, Catatumbo, Northern Venezuela (Rancho Grande), Guiana, Imerí, Napo, Eastern Peru and the Madeira-Tapajós refugium (moved slightly westward and called Rondônia-Aripuanã), and Belém-Xingu. Additional refugia were proposed at Paria and Imataca in eastern Venezuela, Olivença and Tefé in the western part of Brazilian Amazonia, and north of Manaus in Central Amazonia (see Fig. 3). This paper also stressed the importance of gallery forests both as refugia and as contact areas during the drier periods. This was compared with the many Amazonian present day forest species which are distributed well into the Planalto of central Brazil by means of the gallery. This paper is the only one so far by a botanist which has sought to map refugia over the entire lowland area. Prance did not consider the Atlantic coastal refugia of eastern Brazil in any detail apart from suggesting that the area is an area of refugia.

In later papers Prance (1978, 1981a) reviewed briefly the botanical data which has been used to discuss refugia, and presented another map of refugia (Fig. 4), which was not greatly different from that of Prance (1973) except to place a greater emphasis on the role of the gallery forests during the Pleistocene. The papers discussed the species diversity of the Amazon forest giving examples from inventories and citing an example of ten sympatric species of *Eschweilera* (Lecythidaceae) on the same hectare of terra firme forest near to Manaus. They also discussed the present day distribution of savannas in Amazonia and the role of gallery forest and forest islands in savanna. The following disjunctions were observed: between Panama and Guiana, for example *Licania affinis* Fritsch (Chrysobalanaceae); between Guianas and western Amazonia, for example *Mouriri oligantha* Pilg.; between Amazonia and Pernambuco, for example *Hirtella bicornis* Mart. & Zucc. and the species cited in Andrade-Lima (1953); between Amazonia and Rio de Janeiro, for example *Couratari macrosperma* A. C. Smith (Lecythidaceae) and between northern South America and eastern Brazil, for example the genus *Stephanopodium*. These disjunctions were explained in terms of changes in forest cover rather than long distance dispersal. These papers also

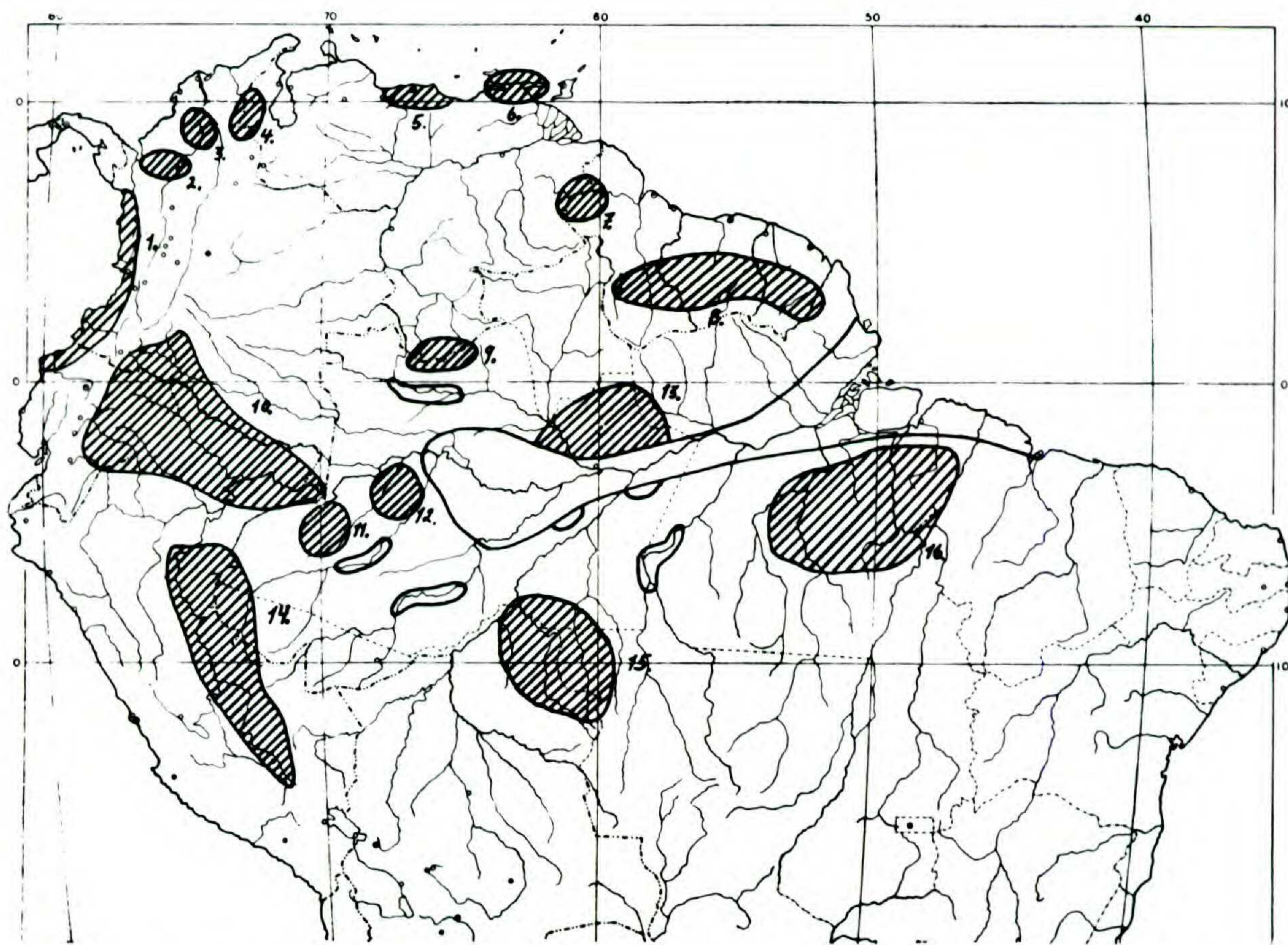


FIGURE 3. The forest refugia proposed by Prance (1973) from a study of endemism in forest species of four woody plant species: 1, Chocó; 2, Nechi; 3, Santa Marta; 4, Catatumbo; 5, Rancho Grande; 6, Paria; 7, Imataca; 8, Guiana; 9, Imeri; 10, Napo; 11, Olivença; 12, Tefé; 13, Manaus; 14, East Peru; 15, Rondônia-Aripuanã; 16, Belém-Xingú.

discussed polymorphic species (ochlopecies) and reasons for their variation and finally centers of species diversity in the lowland forests were identified.

Soderstrom and Calderón (1974) studied the tribes of bambusoid grasses Olyreae and Parianeae, especially the genera *Diandrolyra* and *Piresia* both of the former tribe. They found that the primitive species of the group occur in the forests of eastern Brazil, particularly in Bahia and north of the Rio Doce in Espírito Santo. They hypothesized that eastern Brazil, particularly Bahia, represents a refugium of the primitive elements of these genera and that migration occurred south along Serra do Mar and northwest into Amazonia. The forest area from Bahia north to the State of Paraíba is considered a refugium for at least some primitive herbaceous bambusoid grasses. They commented briefly that Amazonia was also populated from the north where the Panamanian-Chocó refugium harbors such primitive grasses as the Olyroid genus *Maclurolyra*.

The distribution of *Piresia* of the Olyreae would certainly support the Bahia refugium theory well. *Piresia* has four species in Bahia and one species in the refugium of Peruvian Amazonia as well as two species which are widespread in northeastern Amazonia and are sympatric in the Guiana refugium area.

Further evidence for a Bahia refugium and other refugia in Atlantic coastal Brazil is given in Mori et al. (1981), which is a study of the distribution of 127 species that occur in the region. Fifty-three and one-half percent of the

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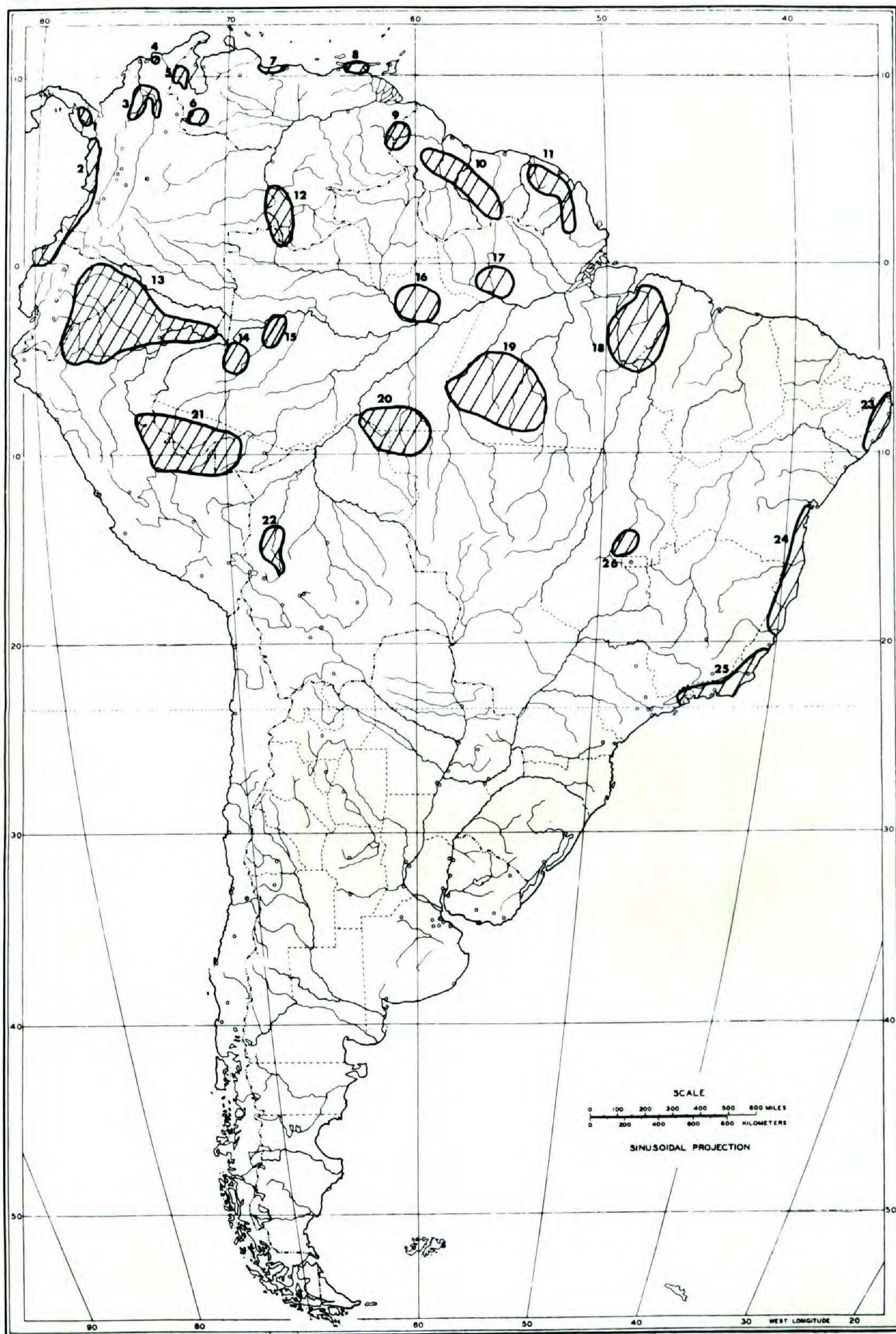


FIGURE 4. The forest refugia proposed by the author currently and in previous publications (Prance, 1978, 1981a): 1, Panama-Darién; 2, Chocó; 3, Rio Magdalena; 4, Santa Marta; 5, Catatumbo; 6, Apure; 7, Rancho Grande; 8, Paria; 9, Imataca; 10, West Guiana; 11, East Guiana; 12, Imeri; 13, Napo; 14, Olivença; 15, Tefé; 16, Manaus; 17, Trombetas; 18, Belém; 19, Tapajoz-Xingu; 20, Air-puanã; 21, E. Peru-Acre; 22, Beni; 23, Pernambuco; 24, Bahia; 25, Rio-Espírito Santo; 26, Araguaia.

TABLE 1. Analysis of 31 species of Memecyleae considered as local endemics by Morley (1975), showing relationships to refugia and habitat, see also Figs. 5 and 6. The refugia of Haffer (H), Vanzolini (V), and Prance (P) are referred to by Morley, and for the Atlantic coast the Serra do Mar dispersal of Müller (M) is used.

A. Endemic species which according to Morley (1975) fit proposed refugia.			
	Refuge	Authors	Habitat Data
<i>Mouriri pseudogeminata</i> Pittier	N. Venezuela	HVP	Open deciduous forest
<i>rhizophoraefolia</i> (DC.) Triana	Imataca (near)	P	Forest
<i>micranthera</i> Morley	Chocó	HP	Forest
<i>pachyphylla</i> Burret	Chocó (+ Gorgona Is.)	HP	Forest
<i>angustifolia</i> Spruce ex Triana	Imerí (near)	HP	Moist caatinga
<i>spruceana</i> Morley	Imerí	HP	Caatinga & disturbed forest
<i>duckeanoides</i> Morley	Manaus	P	Forest on terra firme
<i>froesii</i> Morley	Manaus (near)	P	No data
<i>Votomita pleurocarpa</i> (Morley) Morley	Olivença (near)	P	Forest on terra firme
<i>monadelphæa</i> (Ducke) Morley	Belém	HP	Forest on terra firme
<i>orbinaxia</i> Morley	Belém	H	Forest on terra firme
<i>Mouriri obtusiloba</i> Morley	Belém (near)	P	No data
<i>arborea</i> Gardn.	Serra do Mar	M	Forest
<i>doriana</i> Morley	Serra do Mar	M	Forest
<i>chamissoana</i> Cogn.	Serra do Mar	M	Forest
<i>bahiensis</i> Morley	Serra do Mar	M	Forest
<i>regelliana</i> Cogn.	Serra do Mar	M	No data
B. Endemic species which "fit none of proposed refugia" (fide Morley, 1975).			
			Habitat Data
<i>Mouriri francavillana</i> Cogn.	Guiana, near coast outside refugium		Forest on terra firme
<i>Votomita guianensis</i> Aubl.	Guiana, near coast outside refugium		Forest on terra firme
<i>Mouriri ambiconvexa</i> Morley	W. Amazonia, Colombia, Rio Apaporis		No data
<i>barinensis</i> (Morley) Morley	Venezuela, Barinas, Ticoporo		Wet forest
<i>dimorphandra</i> Morley	Central & S. Amazonia, Manaus-Porto Velho		Forest on terra firme
<i>eugeniaefolia</i> Spr. ex Tr.	Central & W. Amazonia, Manaus-Rio Vaupés		Igapó
<i>exadenia</i> Morley	Peru, Loreto: Rio Huallaga		Dense forest
<i>floribunda</i> Markgraf	Peru, Amazonas, Pongo de Manseriche		Forest on terra firme
<i>longifolia</i> (HBK) Morley	Venezuela, Amazonas		Moist forest
<i>micradenia</i> Ducke	Brazil, São Paulo de Olivença		Forest on terra firme
<i>monopora</i> Morley	Brazil, Amazonas, Ig. Jandiatuba		Forest on terra firme
<i>tessmannii</i> Markgraf	W. Amazonia, Peru, Pongo de Manseriche		Forest on terra firme
<i>uncithecæa</i> Morley & Wurdack	Venezuela, Amazonas		White sand scrub
<i>orinocensis</i> Morley	Venezuela, Amazonas, Río Orinoco		Bank of river

forest species are shown to be endemic there and the distributions indicate a clear separation of a northern and southern refugium in the region. The region of Rio de Janeiro has many endemics that separate it from that of southern Bahia-northern Espírito Santo which is another area of high endemism.

Morley (1975) has made the most detailed, botanically based, critique of the refuge theory based on the distribution of species of Memecyleae (Melastomataceae). Morley argued that present day climate distribution could account for the distribution of all species of the group except *Mouriri oligantha* Pilg. He favored habitat preference and tolerance ranges over climatic variations as the cause of speciation in the Memecyleae. However, he cited several other cases in his paper which fit well into the refuge theory. Since the Memecyleae are a woody group primarily of forest, and are well worked out taxonomically with readily recognizable species as defined by Morley, they are discussed in some detail here. Morley's discussion is based on the refugia proposed by Haffer (1969), Vanzolini and Williams (1970), and Prance (1973).



FIGURE 5. Distribution map of Memecyleae (Melastomataceae) which according to Morley (1975) fit well into refugia: a, *Mouriri panamensis*; b, *M. micranthera*; d, *M. pachyphylla*; e, *M. rhizophoraefolia*; f, *M. froesii*; g, *M. angustifolia*; h, *M. spruceana*; i, *Votomita pleurocarpa*; j, *Votomita monadelphae*; k, *Mouriri duckeanoides*; n, *V. orbinaxia*; o, *Mouriri chamissoana*; p, *M. obtusiloba*; q, *M. bahiensis*; r, *M. regeliana*; s, *M. arborea* and *M. doriana*; t, *M. pseudogeminata*.

Table 1 is an analysis of 31 species of Memecyleae which are listed by Morley as local endemics, and these species are also mapped in Figs. 5 and 6. There are 17 species which fit near to the refugia discussed (Fig. 5), and 14 local species which, according to Morley, do not fit well into the refugia (Fig. 6). The 14 local species which do not fit according to Morley need to be considered further. Eleven of these species occur quite near to the refugia of Prance (1973) and only three are completely outside refugium areas: *M. eugeniaefolia* Spruce ex Triana, a species of black water igapó with a typical distribution on the Rio Negro of many species adapted to that habitat; *M. ambiconvexa* Morley, a species without habitat data, but probably of white sand caatinga; and *M. dimorphandra* Morley, a rain forest species with rather a wide distribution from the Manaus refugium area south to Porto Velho in the Rondônia refugium. The first two species are adapted to specific habitats other than the rain forest and cannot be used as evidence for or against refugia, but show one of the other types of speciation

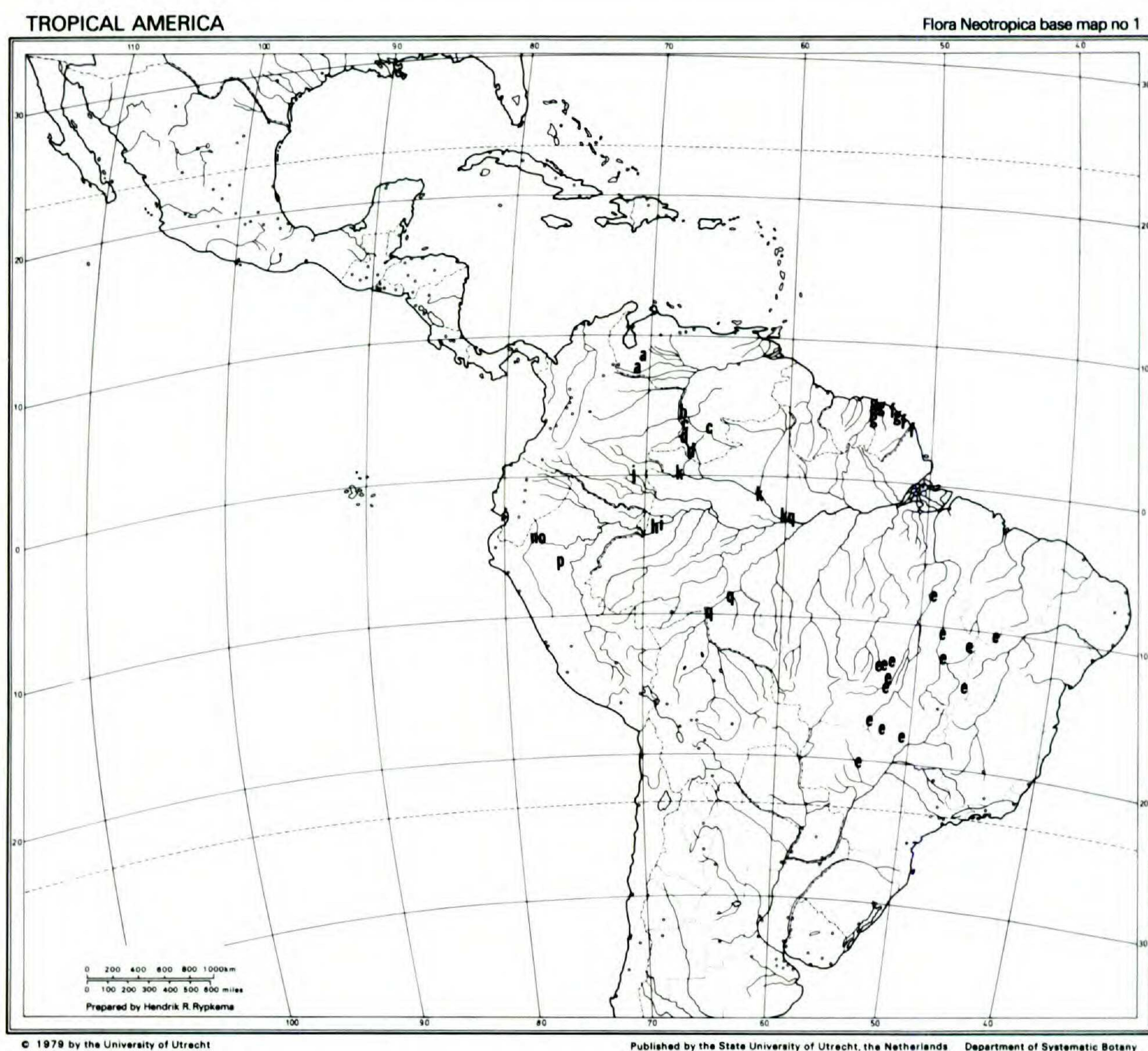


FIGURE 6. Distribution map of Memecyleae (Melastomataceae) which according to Morley (1975) do not correspond well to refuge theory, and *M. elliptica* of Central Brazil: a, *Mouriri barinensis*; b, *Votomita orinocoensis*; c, *Mouriri longifolia*; d, *M. unci-theca*; e, *M. elliptica*; f, *M. francavillana*; g, *Votomita guianensis*; h, *Mouriri micradenia*; i, *M. monopora*; j, *M. ambiconvexa*; k, *M. eugeniae-folia*; n, *M. tessmannii*; o, *M. floribunda*; p, *M. exadenia*; q, *M. dimorphandra*.

which occurs, adaptation to present day habitats. Nine of the other eleven endemic species said to fall outside refugia are forest species and must be considered in the studies of refuge theory, and two are local habitat adaptations (*M. unci-theca* Morley & Wurdack to white sand scrub of the Orinoco region and *Votomita orinocoensis* Morley to rocky riverine habitats of the Rio Orinoco). The nine forest species are discussed individually below:

1. *M. barinensis* Morley is southwest of the Catatumbo refugium of Prance (1973) and nearer to the Apure refugium of Brown (1976), which is recognized here.

2. *M. longifolia* (HBK) Morley is north of the Imerí refugium of Prance (1973) and within the Ventuari refugium of Brown (1976), and the Imerí area as redefined here.

3. *M. guianensis* Aubl. and *M. francavillana* Cogn. are distributed just north

of the Guiana refugium of Prance (1973), Brown (1976), and within the area designated as the Guiana refugium in the present work.

4. *M. tessmannii* Markgraf and *M. floribunda* Markgraf are just south of the Napo refugium of Prance (1973) and Brown (1976). These two species occur at the Pongo de Manseriche, an area of high endemism which has been included in the Napo refugium as defined here.

5. *M. exadenia* Morley occurs very slightly outside the east Peru refugium of Prance (1973) in an area of relatively low botanical endemism.

6. *M. micradenia* Ducke and *M. monopora* Morley occur near to São Paulo de Olivença, Brazil, only slightly north of the Olivença refugium of Prance (1973), which has been moved in the present work to include the area where these two species occur.

The data from the endemic species of Memecyleae help to define refugia better through slight modification of earlier proposals rather than contradict the refuge theory. The data demonstrate centers of endemism and the possible location of refugia.

In addition to considering endemics, Morley discussed two species pairs and one disjunct species of *Mouriri* which are further supportive of the refuge theory. *Mouriri crassifolia* Sagot is a common species of the Guianas, Amapá, and eastern Pará, and its closest relative *M. ficoides* Morley is common around Manaus. The same distribution occurs in *M. dumetosa* Cogn. of the Guianas and *M. densifoliata* Ducke from around Manaus. These appear to be two vicarious species pairs and a logical explanation of their separation into two populations is by the changes in forest cover during dry periods.

Mouriri oligantha Pilg. is divided into two distinct populations, one in the Guianas and the other in eastern Peru. Morley proposed that this species had a continuous distribution at a time of greater humidity and was distributed around the embayment of Amazonia and was later broken into two populations by a drier climate cycle. This type of distribution in the Guianas and eastern Peru is paralleled in many other plant distributions (e.g., *Couepia parillo* DC, Chrysobalanaceae; *Tassadia guianensis* Decne, Asclepiadaceae, see Pereira (1977)), and is good evidence of the effect of drier phases in Central Amazonia.

In addition to the local and disjunct species mentioned above, *Mouriri* has three widespread polymorphic ochlopecies with much local variation throughout their range, *M. grandiflora* DC., *M. vernicosa* Naud., and *M. guianensis* Aubl., with their maximum differentiation in the Guianas. This variation can also be accounted for by adaptation to climate changes and will be discussed further below.

Although Morley argues that the present day climate differences could account for all the geography of *Mouriri* except *M. oligantha*, it seems that his data can be interpreted differently to show clear evidence of the effect of Pleistocene climate changes. Distribution patterns that correlate with present day climate do not negate the idea of Pleistocene refugia.

Sastre (1976) made a study of the open vegetation areas of the Guianas with particular attention to the savannas and mountain tops. He found that the Guiana savannas individually show no endemism, but that the sandstone mountains over

1,000 m in altitude show considerable endemism. He estimated that forty percent of the species of granite outcrop also occur in the lowland savannas, and that fifty-five percent of the species were confined to mountain tops. Of these fifty-five percent, forty percent are rock specific. He discussed the problems of the distribution of mountain top savanna species, which are often divided into populations separated by 300 km or more of forest. Sastre observed that long distance dispersal by birds answers some, but not all of these distributions and called on the spread of savanna in dry periods to explain some of these distributions. He also recognized the Guiana mountains as a center of species differentiation for species of open habitats because of their subsequent isolation as small islands of vegetation where differentiation between islands took place.

It is interesting to note that many species of savanna and other open areas have obvious adaptations for long distance dispersal in marked contrast to those of the rain forest. This limits the use of distribution data from savanna species to draw conclusions about savanna changes. For example, Macedo and Prance (1978) showed that 75.67% of species of Amazonian white sand campina have this capacity for long distance dispersal by birds but also bats or the wind.

Descamps et al. (1978) in part of the same study as Sastre (1976) worked on the plants and animals of savannas and rock outcrops of French Guiana. They divided the Guianas into three biogeographic subregions based on the distributions of various forest species. They concluded that speciation of forest species in the Guianas took place in more than one center and that during the times of dry climate the Guianas were broken up into at least three refugia rather than the single one proposed by Haffer (1969) and Prance (1973). They suggested that the easternmost refugium is located north of the Tumucumaque mountains between Tampoc and Camopi rivers around Saül and between the Comté and the Appro-uaque. This is farther northwest of the Oiapoque refugium of Brown (1976).

The most detailed refuge analysis for French Guiana is that of de Granville (1981). He postulated a large central refugium in the zone of the present day high rainfall where there is greatest vegetational diversity centered around Saül (Fig. 7). The refugium occupied most of central and eastern French Guiana with its northern limit in the Kaw range and southern one in the Inini-Camopi mountains and extending eastward into Amapá Territory of Brazil. He cited as evidence many interesting endemics from the region such as *Elephantomene eburnea* Barneby & Krukoff (Menispermaceae), and four different species of *Psychotria* (Rubiaceae). The Saül region also has a number of species, such as *Oedematopus octandrus* Planch. & Triana, which are widely disjunct in other areas and provide evidence of isolation. De Granville believes that on the basis of vegetation distribution that the later dry period of the recent Holocene (4,400–2,200 B.P.) also had an impact on the vegetation not by causing new savanna, but by delaying the advance of the forest.

De Granville also discussed remnants of an arid flora of French Guiana in today's humid climate. The arid vegetation is now separated into discrete isolated sites acting as refugia for the arid species. The arid vegetation type of three coastal savannas is of limited use for refuge study because it was flooded as recently as 6,000 years B.P. However, the rock outcrops (inselbergs) and emergent rocks in rivers are much older refugia for arid region species. De Granville provided fur-

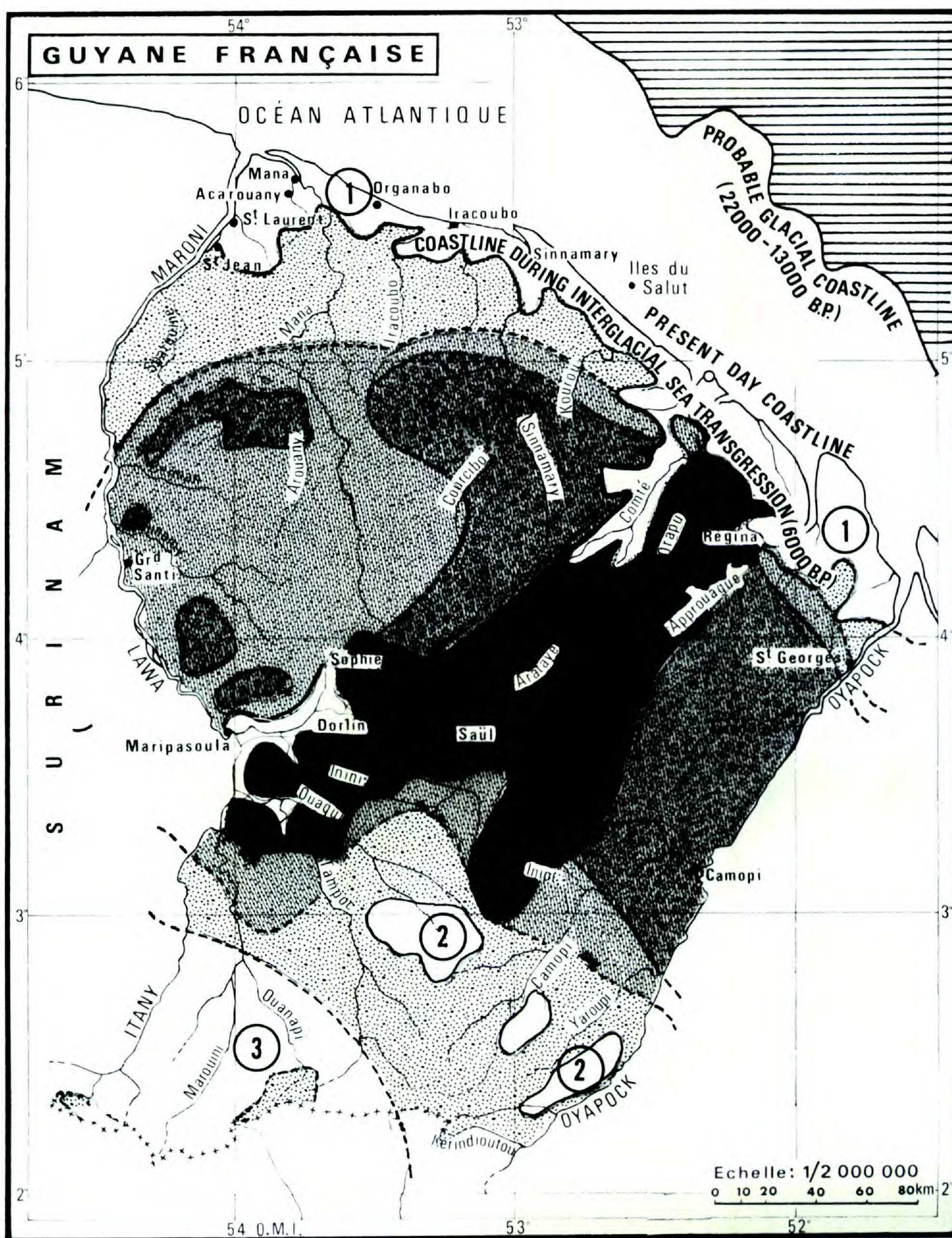


FIGURE 7. The Pleistocene forest refugium proposed by de Granville (1981) for French Guiana.

ther data about the vegetation outcrops of the Tumac-Humac region studied by Sastre (1976) and Descamps et al. (1978). Some of the arid adapted species are equally saxicolous, savannicolous, and of the coastal savannas, e.g., *Borreria latifolia* (Aubl.) K. Schum., *Stylosanthes hispida* Rich., and *Xyris fallax* Malme. Other species are confined to one of these arid vegetation types.

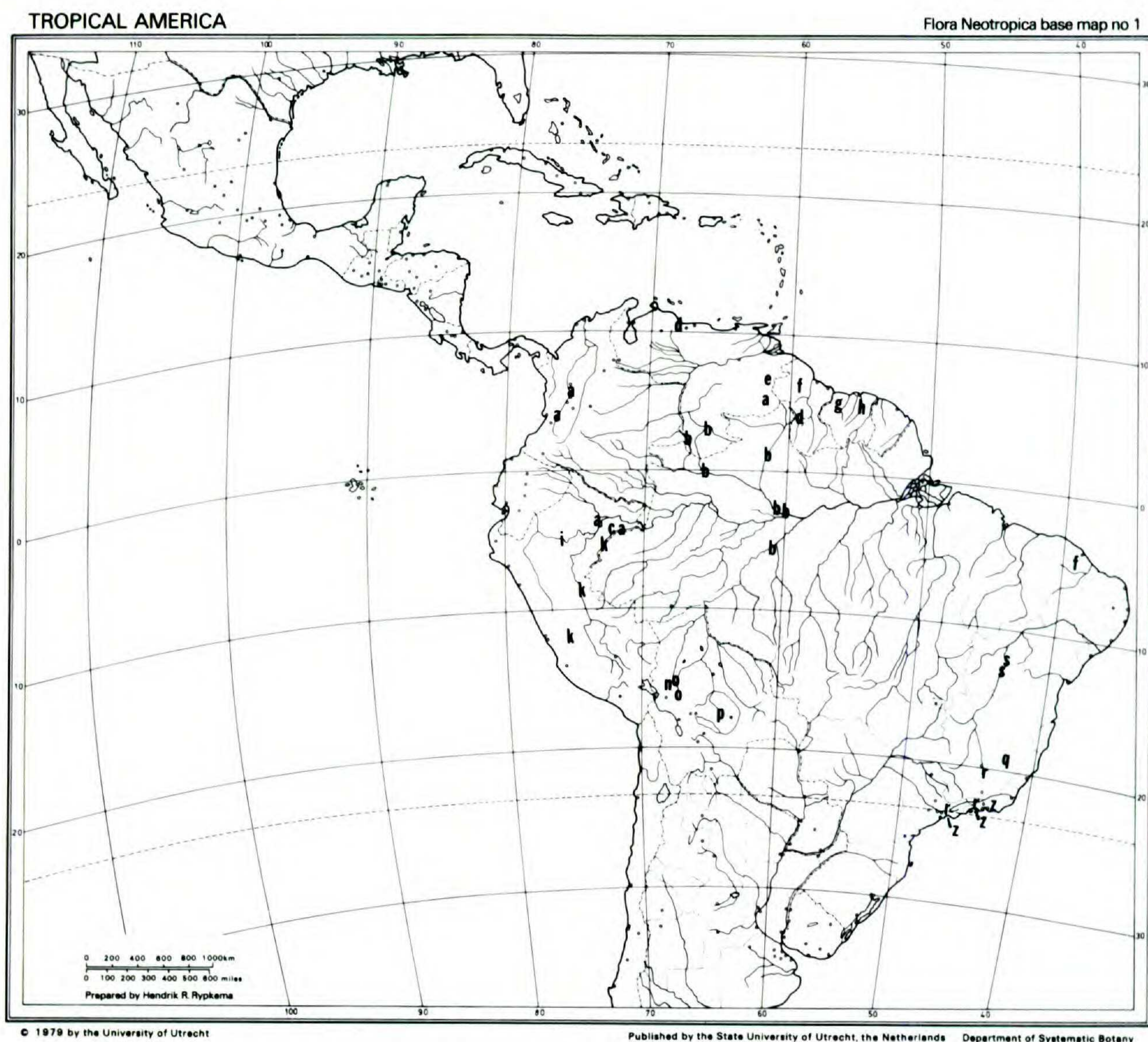


FIGURE 8. The distribution of *Trigonía* (Trigoniaceae) discussed by Lleras (1978) in connection with refuge theory: a, *T. sericea*; b, *T. sprucei*; c, *T. prancei*; d, *T. subcymosa*; e, *T. bracteata*; f, *T. villosa* var. *macrocarpa*; g, *T. coppenamensis*; h, *T. candelabra*; i, *T. macrantha*; k, *T. killipii*; n, *T. floccosa*; o, *T. echiteifolia*; p, *T. boliviana*; q, *T. eriosperma* subsp. *simplex*; r, *T. paniculata*; s, *T. nivea* var. *fasciculata*; z, *T. rytidocarpa*.

De Granville also discussed the forest canopy, which he considered as a refuge for epiphytes such as *Aechmea setigera* Mart. and *Topobea parasitica* Aubl.

Forero (1976) revised the American species of *Rourea* (Connaraceae) and provided clear distribution maps of all species. This paper is cited by Simpson and Haffer (1978), but it does not discuss the distribution of *Rourea* in terms of refuge theory. The distributions are related to the phytogeographic regions of Ducke and Black (1953) and show that the lowland forest of Amazonia is varied and the phytogeographic subdivisions are confirmed by *Rourea*. *Rourea* has many riverine species of inundated forest which are not good examples for the discussion of refugia. However, a few local species fall exactly into refugia areas: *R. ligulata* Baker in the Belém refugium; *R. duckei* Huber in the Guiana refugium; *R. cuspidata* Benth. ex Baker var. *densiflora* (Steud.) Forero in the east Peru refugium; and *R. sprucei* Schellenb. var. *subcoriacea* Forero in the Imerí refugium. Also *Rourea glabra* has an interesting disjunct distribution occurring in

TABLE 2. Correspondence between refugia of Prance (1973) and taxa of *Trigonia*. Species marked with an asterisk are also widespread outside the refugium listed.

Nechi	<i>T. rugosa</i> Benth.*, <i>T. sericea</i> HBK*
Nechi, Santa Maria	<i>T. eriosperma</i> subsp. <i>membranacea</i> (A. C. Sm.) Lleras*
Catatumbo	<i>T. rugosa</i> Benth.*
Paria & Guiana	<i>T. nivea</i> Camb. var. <i>nivea</i> *
Imataca	<i>T. bracteata</i> Lleras, <i>T. reticulata</i> Lleras
Guiana	<i>T. hypoleuca</i> Griseb., <i>T. coppenamensis</i> Stafleu, <i>T. subcymosa</i> Benth., <i>T. candelabra</i> Lleras, <i>T. villosa</i> Aubl. var. <i>villosa</i> (plus 3 non-edemic taxa)
Napo	<i>T. macrantha</i> Warm., <i>T. prancei</i> Lleras (plus 2 non-endemic species)
Manaus	<i>T. nivea</i> var. <i>pubescens</i> (Camb.) Lleras, <i>T. spruceana</i> Benth. ex Warm.*
E. Peru	<i>T. killippi</i> Macbride
E. coast Brazil forests	<i>T. rotundifolia</i> Lleras, <i>T. rytidocarpa</i> Casar., <i>T. paniculata</i> Warm.

Central America, Colombia, Venezuela, and Roraima, Brazil and disjunct in eastern Brazil in the vicinity of Rio de Janeiro.

Lleras (1978), in a monograph of the Trigoniaceae, treated the refuge theory in some detail basing his discussion on the refugia of Haffer (1969) and Prance (1973). He suggested that the distribution of Trigoniaceae offers further support to the refuge theory since the centers of distribution coincide with those of the four families studied by Prance (1973). The Trigoniaceae has two distribution centers: southeastern Brazil around Rio de Janeiro, Venezuela, the Guianas, and northern Amazonia. The northern group has been most strongly affected by isolation into refugia. Table 2 shows the correspondence between the refugia of Prance (1973) and taxa of *Trigonia*. Fourteen of the total thirty taxa recognized by Lleras correspond well to refugia (Fig. 8) and another six more widespread taxa have their distribution centered on refuge areas, showing that the distribution of the genus does indeed coincide well with postulated refugia.

In addition to the above species of *Trigonia*, which correspond to refugia, Lleras drew attention to the species *T. boliviana* Warm., *T. floccosa* Rusby, and *T. echitifolia* Rusby, which are all endemic to the eastern limit of the Andes in Bolivia. He also commented that with further paleobotanical work in the Amazon basin, a somewhat different distribution of refugia may have to be postulated; these aspects are discussed further below.

One of the most detailed botanical studies of the refuge theory was done in Mexico and Central America by Toledo (1976, 1981). In Mexico there are many more evidences of Pleistocene climatic changes, which are summed up in considerable detail by Toledo. Graham (1981) provided much palynological evidence for the climatic changes in Mexico. Toledo (1976) pinpointed five refugia for Mexico and northern Central America. These were based mainly on evidence from centers of endemism and the distribution of endemic species in a similar way to methods used in Amazonia. Toledo also pointed to other botanical evidences in Mexico:

1. The distribution of temperate elements in areas of tropical rain forests, for example *Quercus* and *Pinus*.
2. The distribution of xerophytic elements in tropical rain forest areas (also one of the evidences discussed by Simpson, 1972).

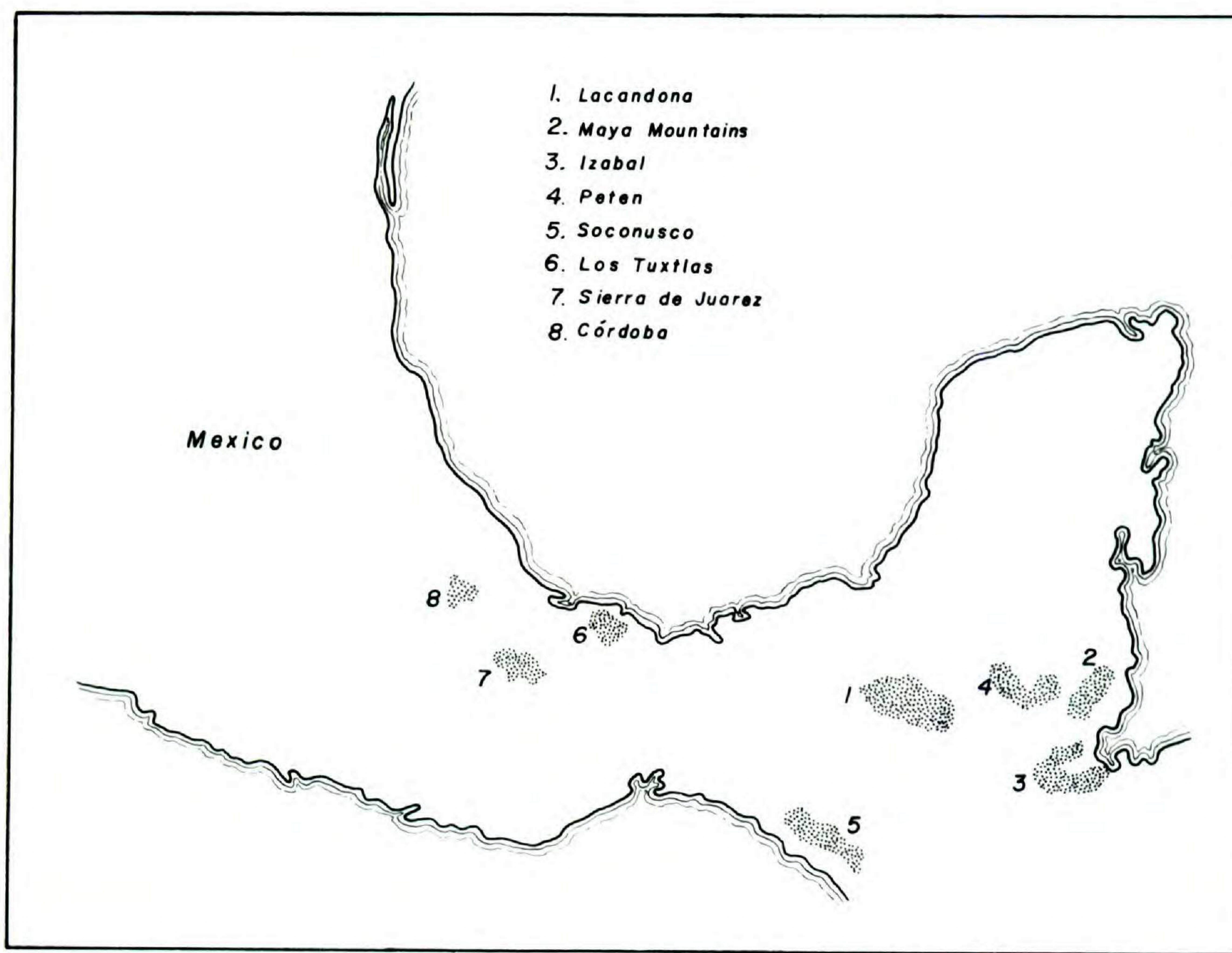


FIGURE 9. The proposed forest refugia in Mexico and adjacent Central America of Toledo (1981). Areas 1–5 are the primary refugia which were also discussed in Toledo (1976) and areas 6–8 are the secondary refugia.

3. The strong tolerance of drought of certain species of the tropical rain forest.

4. Distribution of tropical rain forest species into the cooler climate zones of today. Many examples of this are given, such as *Guarea chichon* C. DC. (Meliaceae).

5. The unusual and differing distribution patterns of the dominant species of the tropical rain forests showing the recolonization capacities of different trees.

6. The latitudinal distribution of tree species.

7. The study of leaf shape and morphology, using the ratio of different types of leaf margin, etc., as an indicator of climate type.

Toledo proposed five refugia for rain forest species during the Pleistocene in Mexico and adjacent Central America (Fig. 9).

1. The Lacandona Region of Chiapas, Mexico.

2. The southeastern portion of Belize in Toledo district including Sierra Maya.

3. Northwest of Sierra Maya around Tikal and Flores in Peten, Guatemala and a part of Cayo District in Belize.

4. The surroundings of Lake Izabal, Izabal Department, Guatemala.

5. The region of Soconusco, Chiapas, Mexico.

The designation of refugia by Toledo is a thorough study with methods which could be applied to Amazonia. The refugia of Central America could have been

important when the recoalescence of the forest occurred because this provided a route for northern species into the northern part of South America. There are some species of Central America with disjunctions well into South America, such as *Licania arborea* Seem. (Chrysobalanaceae), a species common in Central America and the extreme north of Colombia which is disjunct into Amazonian Peru. This type of distribution pattern can probably be explained by the Pleistocene history of the region.

Toledo (1981) discussed further the Mexican and Central American refugia. He gave details of the five refugia defined previously and termed them primary refugia. These areas have the most evidence that they in fact remained as intact units of forest during the arid phases. In his 1981 paper he mentioned three further areas that, because of their high rainfall (over 3,500 mm present day), could also have been refugia for rain forest species. These secondary refuge areas (Fig. 9) were:

1. Sierra de los Tuxtlas in Veracruz.
2. Sierra de Juárez in Oaxaca.
3. The lower slopes of the Sierra Madre in the region of Córdoba in Veracruz.

Further botanical work is needed to determine the role of these areas. The region of Tuxtlas, for example, has endemic species of *Inga*, *Erythrina*, *Pithecellobium*, *Sophora*, *Ficus*, *Tillandsia*, *Heliconia*, *Olmeca*, etc., as well as sub-specific taxa of various plants which would indicate recent isolation.

Gentry (1978) in a general paper about the floristics of Pacific Tropical America, discussed briefly the richness and importance of the Chocó refugium as a source of material for the species rich forest of Panama. His work has shown that the tropical moist forest of Panama is by far the most species rich area in Central America, and its historical relationship to the Chocó refugium is important.

Gentry (1979) discussed refugia in much more detail in relation to the distribution of neotropical Bignoniaceae. He observed that some species of Bignoniaceae fit well into the refugia patterns of Haffer (1969), Prance (1973), and Brown (1976), and also into the phytogeographic regions proposed by Prance (1977) with a slight modification of the western region. While some do fit into the presently accepted pattern of refugia, Gentry observed that many others do not, and also that the collecting sample is extremely poor. He cited, in a table, 19 species of Amazonian Bignoniaceae which were presumed to be local endemics and which have since been collected in far distant places, for example *Tabebuia incana* Gentry first known from Manaus, Brazil, which was collected for the second time on the Río Ucayali in Peru. Such collections show that some species previously considered as local endemics (and used as such for studies of refugia) are in fact widespread. Gentry called the Manaus refugium of Prance (1973) 'controversial' since it was not recognized by many zoogeographers and since 10 species of Bignoniaceae thought to be Manaus endemics have been collected later outside that region. Gentry, however, points out the importance of the consideration of dispersal mechanism of any plant under study and that wind dispersed canopy lianas are perhaps too easily dispersed to have retained present day distribution patterns which can be correlated with refugia. He also provided a good example of the contrasting distribution patterns of the light seed wind dispersal

and heavy fruited mammal dispersed Bignoniaceae which confirm that present day distribution patterns are quite different in the two dispersal groups.

An interesting aspect of Gentry's paper is a discussion of dry forest vegetation species of Bignoniaceae as examples of species in present day 'reverse refugia.' Dry forest areas have contracted today leaving isolated patches which act as contemporary refugia for a different group of species which includes many species of Bignoniaceae, a family well adapted to drier areas throughout its range. Gentry suggested that dry forest Bignoniaceae do seem to provide evidence for the existence of 'reverse refugia.' Many species of Bignoniaceae are restricted to dry forest scattered around the fringes of Amazonia especially in the Interandean valleys of Colombia and Peru and in Central America. Some species, for example *Tabebuia impetiginosa* (Mart. ex DC.) Standl., show little differentiation between their various isolated populations, but others like *T. ochracea* (Cham.) Standl., which has been divided into various taxonomic subspecies by Gentry, appear to be actively differentiating at present. These subspecies correspond to the different contemporary dry forest refugia. Gentry cited further examples of variability in dry forest species and observed that further study of these and similar dry forest disjuncts from other families, from the aspect of refugia should prove useful in the investigation of evolutionary mechanisms in tropical plants.

Gentry (1981) furnished further details about the northwestern part of South America basing his conclusions on his own work in Bignoniaceae and that of Sota (1972) and Lellinger (1975) on pteridophytes. He concluded from his study of the plant diversity of Chocó that there is an unusually high species diversity with a strikingly high rate of endemism (20% of the species studied) concentrated in two or possibly three centers. The closest generic relationship of the flora is with that of Amazonia indicating an Amazonian origin of the flora, but the closest species relationship is with Central America. Many Amazonian families and genera have one or a few outlier species in Chocó, for example Caryocaraceae, Trigoniaceae, *Cariniana* (Lecythidaceae), *Qualea* (Vochysiaceae). Gentry listed 19 examples of species pairs in a table. Gentry concluded that botanical evidence is consistent with the persistence of one or more refugia in Chocó during the Pleistocene dry periods. The endemics of the region fall readily into a northern and a southern group divided near the southern boundary of the department of Chocó in Colombia which indicates a separation into at least two separate refugia.

Another interesting and original part of Gentry's paper is that of evidence from the mangrove flora. The Pacific mangrove flora is markedly richer in species than the Caribbean-Atlantic side. There are six more species in the Pacific mangrove which were confined to the moist areas and restricted in range during the Pleistocene. The fossil record shows a wider distribution of some, for example *Pelliciera rhizophorae* Pl. & Tr., which later became restricted to the Chocó region.

Gentry also presented more evidence about 'reverse' contemporary savanna refugia by discussion of differentiation and subspeciation in *Tabebuia ochracea* (Cham.) Standl. and populational differentiation in species of *Tecoma*. Present day isolation of these species in savannas has allowed differentiation to begin.

Steyermark (1979) presented an extremely detailed account of refugia and dispersal centers in Venezuela. This is the most detailed account of any small

area of South America from the point of view of plant species endemism. In common with many of the other authors already cited, Steyermark began by pointing out the limitations of the present day collection sample for the pinpointing of dispersal centers. He considered the sample in Venezuela as very inadequate even though it is one of the better collected areas of tropical America. Steyermark estimated that the Venezuelan flora consists of between 15,000 and 20,000 species of vascular plants. He outlined well the need to consider the present day geology, physiography, and climate together with the climatic changes of the past. He regards the geological formations and present day physiography as a primary factor in present day plant distribution and endemism, and the historical climate changes as a secondary, but, nevertheless, important factor.

Steyermark differentiated between highland and lowland refugia and pointed out that the highland refugia are associated with mountains, were selected on the basis of the unique floras of various mountains and are not necessarily associated with the climate changes of the recent past. The lowland areas of refugia are, however, associated with climate changes of the past. The principal areas of plant endemism in Venezuela are: the Andes, the Coastal Cordillera, the Serrania del Interior, the Pantepui area, the Gran Sabana, and the edaphic lowland savannas.

Steyermark (1981) outlined the principal forest refugia which have preserved elements of the lowland tropical flora (Fig. 10). These are found in five regions: 1) the coastal Cordillera, 2) the Sierra de Imataca and Altiplanicie de Nuria, 3) the San Camilo forests of Estado Apure in western Venezuela, 4) the forests of lowland elevations in the Catatumbo region and adjacent areas in the Maracaibo basin, and 5) some lowland areas of Guayana including the major refugium of Pantepui.

1. The coastal Cordillera contains nine separate refugia (see Fig. 10) including one on the island of Margarita. There are many wide disjuncts to the south, southeast, and southwest. The close relationship of these areas with the forest of the south of Venezuela indicates that it must have had previous contact perhaps at the height of the Pleistocene humid period or through gallery forest. Steyermark cited numerous examples of both the endemic species and the isolated disjuncts. Species such as *Froesia venezuelensis* Steyermark & Bunting, *Qualea pittieri*, *Stephanopodium venezuelanum* Prance are good examples of species of predominantly southern genera which occur in the northern refugia. The area of Steyermark's coastal refugia include Rancho Grande and the Paria refugia of Prance (1973), Brown (1976), and others, and Steyermark has broken this down with a thorough examination of the vegetation.

2. The Andean area in the west of Venezuela contains several refugia and dispersal centers all of which are physiographically associated with the mountain ranges. The largest refugium is that of Catatumbo, southwest of Maracaibo, which also corresponds to the refugium of Haffer and later authors. Steyermark points out that many species of Amazonian distribution reach their northernmost limits in the Catatumbo area, for example, *Faramea capillipes* Muell. Arg. (Rubiaceae).

3. The San Camilo area in the west of Apure was not suggested as a refugium by previous authors, although Brown's Apure refugium includes it. Steyermark listed numerous species of Amazonian affinity in this region such as *Licania latifolia* Benth. (Chrysobalanaceae) and *Dichapetalum latifolium* Baill. (Dicha-

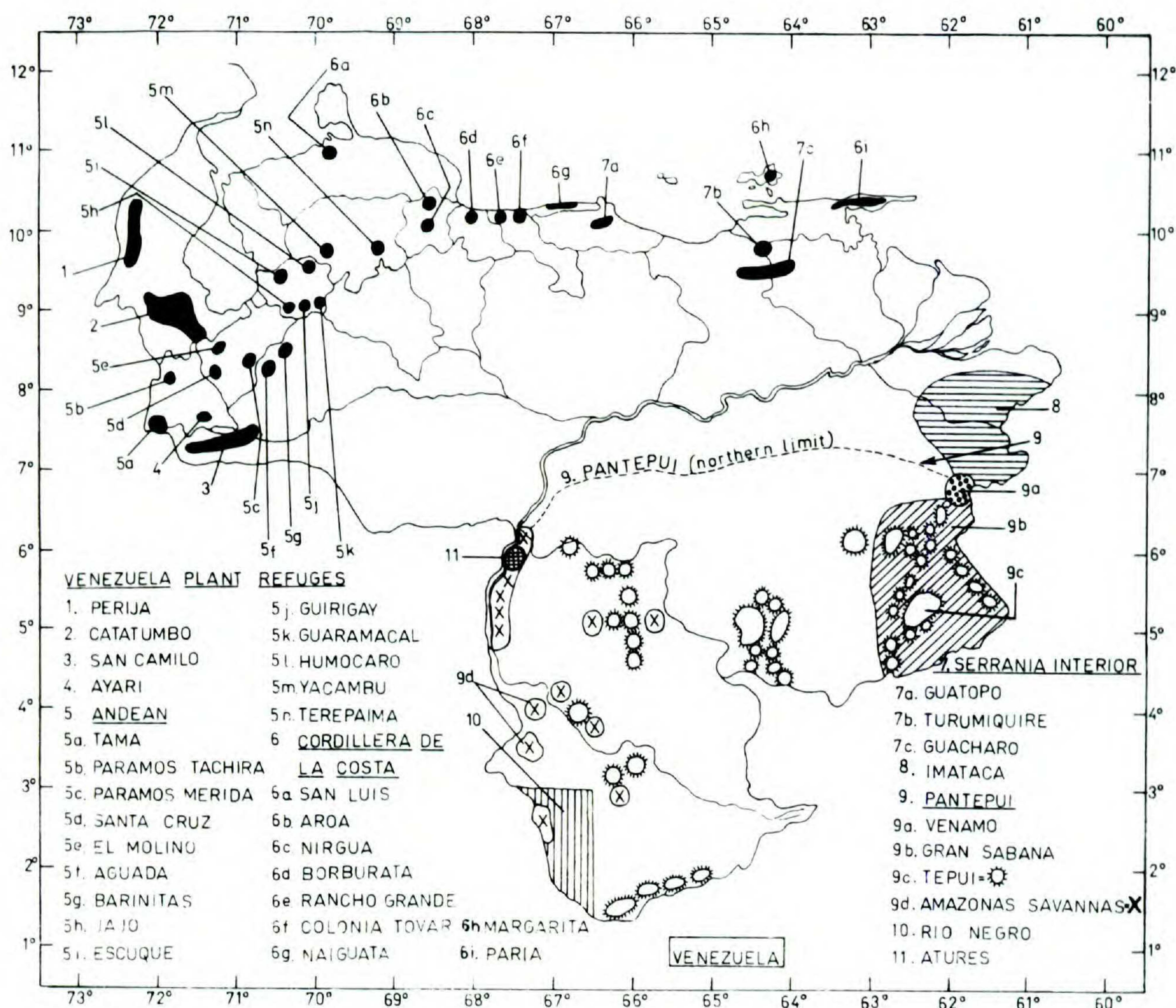


FIGURE 10. The proposed forest refugia (numbered areas) of Steyermark (1981) and location of Tepuis and Amazonas savannas.

petalaceae). *Myrocarpus venezuelensis* Rudd (Fabaceae) also occurs in the San Camilo refugium and is a vicariant species of a genus with the other two species in southern Brazil and Paraguay. Several other small lowland areas around the foothills of the Andes, such as the Ayari refugium in Tachira, are also pinpointed by Steyermark (see Fig. 10).

4. The Imataca refugium is situated just north of Venamo and includes the Altiplanicie de Nuria. This corresponds to the Imataca refugium of Prance (1973), which is extended into Guyana, and also of Brown (1976). The Imataca area has an interesting flora which is intimately associated with the lowland tropical element of the Guianas and Amazonia. Steyermark (1981) furnished a long list of species restricted in Venezuela to the Imataca refugium, as well as a list of endemics such as *Licania latistipula* Prance (Chrysobalanaceae), *Dilkea magnifica* Steyerm. (Passifloraceae), and a list of disjuncts such as *Passiflora spinosa* Mast. otherwise common in western Amazonia.

5. Pantepui as defined in Steyermark (1979) includes the sandstone tops of the Guayana highlands and Gran Sabana in the nearby savanna area. This area includes the Roraima, Ventuari, and Imerí refugia of Brown (1976) and also var-

ious lowland edaphic savannas and igneous lava formations in southern Venezuela. Steyermark stressed the edaphic variability and early history of the region as a cause of much of the endemism that defines his various refugia and dispersal centers in this region. It is interesting that the lowland edaphic savannas of this region have rather a high endemism in contrast to the savannas scattered throughout much of lowland Amazonia. Steyermark pointed out that only 30 genera or 8.5% of the 459 genera are endemic to the summits of the Pantepui, and emphasized the number of summit species which also occur on the slopes. He proposed that distribution from the lowlands to the summits had been much more important than the reverse, which was contrary to the proposals of various previous workers. Within the Pantepui region Steyermark proposed six refugia or dispersal centers:

- a. The Guayana highlands refugium with an east-west subdivision.
- b. The Gran Sabana dispersal center.
- c. The Amazonian savannas of the Río Guainía region such as the Pacimoni savannas and other edaphic savannas on sandy soils.
- d. Atures dispersal center, an edaphic center on igneous rock in the Puerto Ayacucho region.
- e. The Río Negro, lowland forest refugium. This contains part of the Imerí refugium of other authors.
- f. The Venamo dispersal center in the Río Venamo/Cuyari region.

Steyermark's papers are accompanied by large species lists from many different plant families in support of his detailed analysis and conclusions about the Venezuelan vegetation. In this work it is important to differentiate between the endemic centers which are rich because they were refugia, and those areas which are rich as edaphic adaptations to some present day and in many cases also long existent habitat such as the sandstone mountain tops. The number of examples cited makes Steyermark's papers by far the most detailed botanical analysis of endemism and species distribution of any area of South America.

Related to refuge theory and Steyermark's detailed analysis of the Venezuelan vegetation are the studies of Eden (1974) and Huber (1981) of the savanna vegetation of Venezuela. Huber defined three types of savanna in the region: 1) the grassy 'llanos' type of the north; 2) the grassy inundated savannas of the Manapiare-Parucito basin and, 3) the Amazonian savannas of central and western Venezuela characterized by a high amount of plant endemism or strictly Amazonian floristic elements. These represent centers of diversification of pre-Quaternary origin on sandy soils. The *Llanos* and the inundated savannas, however, are modern relicts of Pleistocene and past Pleistocene climate fluctuations of the hylaea. They show strong floristic relationship of extra-Amazonian savanna types such as the *Llanos*. The important study by Eden (1974) on the paleoclimatic influences on the development of savanna in southern Venezuela treated savannas of the llanos type located along the Orinoco river. Eden proposed that paleoclimatic changes caused the origin of three savannas which he visited. These studies point to the need to distinguish between the different types of savanna in any discussion of the vegetational history of northern South America.

Plowman (1979) considered the biogeography of the genus *Brunfelsia* (Solanaceae) and commented that the complex patterns of distribution of the species

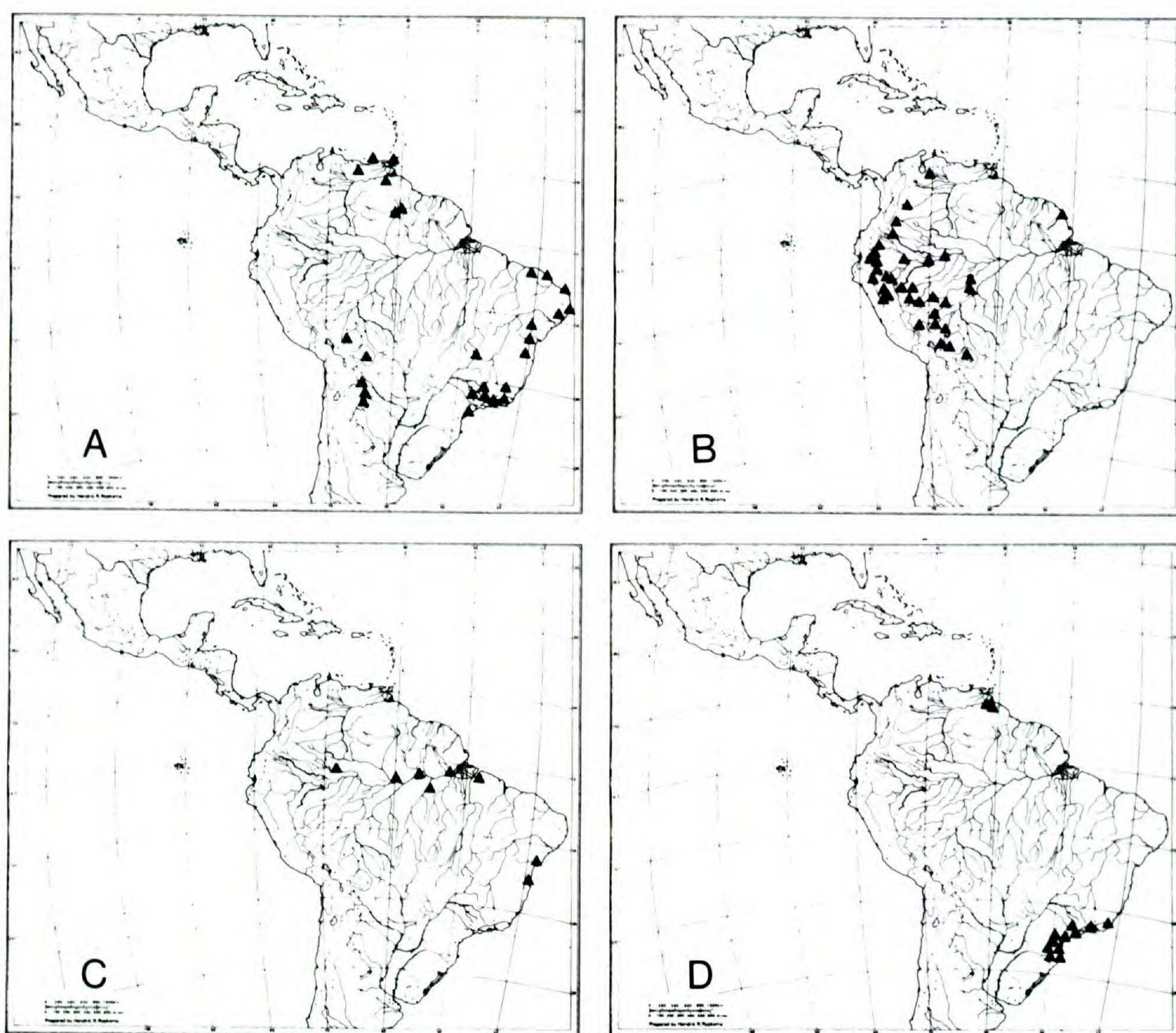


FIGURE 11. Distribution of taxa of *Brunfelsia* (Solanaceae) from Plowman (1979): A, *B. uniflora*; B, *B. grandiflora*; C, *B. martiana*; D, *B. pauciflora*.

of the circum-Amazonian region can only be understood in the context of the past geological and climatic history of South America. A number of taxa of *Brunfelsia* occur in the Amazonian refuge areas, and a number of wide disjunctions occur in the genus. For example, *B. martiana* (Fig. 11) is disjunct between Amazonia and the coastal forests of Bahia, and *B. amazonica* Morton is endemic to the vicinity of Manaus. Plowman concluded, on the basis of the number of local endemics, that the Chocó region has been little changed climatically since before the uplift of the Andes. The most striking Amazonian disjunct is *Brunfelsia grandiflora* D. Don subsp. *schultesii* Plowman, which is widely distributed in the Andean foothills from Venezuela to Bolivia but absent from Central Amazonia and re-occurs in a disjunct population in Amapá, Brazil. The number of endemics in the coastal forest of Brazil as well as the disjuncts with Amazonia and the north, such as *B. pauciflora* (Cham. & Schlecht.) Benth., are evidence of the stability of the Atlantic coastal forests of Brazil. *Brunfelsia pauciflora* (Fig. 11) is common in the Atlantic coastal forests of Brazil and also in the Imatacá refugium in Venezuela. The distribution patterns in *Brunfelsia* correspond well to the forest refugia and Plowman's paper adds further useful botanical evidence of the

influence of the Pleistocene climate changes on the distribution and evolution of plant species. The work of Plowman is interesting because it discusses the isolation of taxa at the sectional, species, and subspecific level.

NORTHEASTERN BRAZIL: CONTEMPORARY REFUGIA

Andrade-Lima (1981) gave a most interesting account of the little known present day forest refugia of the predominantly arid northeastern region of Brazil. Most of the area is covered by the xeric caatinga vegetation. However, forest has persisted on some hills which attract cloud moisture and therefore also have a cooler climate than the surrounding caatinga. These forest patches on hills, termed *brejos* in Brazil, are in a refuge situation. Andrade-Lima listed over twenty such *brejos* which can extend to as low as 500 m (Fig. 12). The species composition of the *brejos* with many Amazonian forest species indicates that they are forest remnants rather than forest formed from easily dispersed colonizers. Such Amazon species as *Manilkara rufula* Miq., *Apeiba tibourbou* Aubl., *Orbignya martiana* B. Rodr., *Parkia platycephala* Benth., and *Virola surinamensis* (Rol.) Warb. are typical of the *brejos*. The *brejos* also contain some forest species of the southern forests of Brazil indicating that they are a most interesting relict with a mixture of isolated species. Southern elements include such species as *Caesalpinia peltophoroides* Benth., *Phyllostylon brasiliensis* Capanema, and *Myrocarpus fastigiatus* Fr. All. Another species of *Myrocarpus* was mentioned by Steyermark (1981) as a species which has become isolated in the northern coastal cordillera refugia of Venezuela.

Andrade-Lima also mentioned the reverse phenomenon of northeastern arid species which are markedly disjunct having now become isolated by extensive forest or cerrados between their populations. Such species include *Anadenanthera macrocarpa* (Benth.) Brenan, *Amburana cearensis* (Fr. All.) A. C. Smith, *Prosopis ruscifolia* Griseb. and *Schinopsis brasiliensis* Engl.

MULTILAYERED DISTRIBUTION PATTERNS

Andersson (1979) discussed the effects of the various contractions and expansions of the rain forest in terms of what he termed 'multilayered distribution patterns.' The effect of the various different climate oscillations are still apparent in present day distribution patterns of *Ischnosiphon* (Maranthaceae) since the effects of the different epochs are found at different taxonomic levels (Fig. 13). Consideration is given to evolution at the sectional, species group, and species level. The patterns of distributions and relationships of each of these levels are discussed by Andersson. Three sections divided into groups of closely related species. The distribution of these species groups are explained in terms of refugia at one time period and that of the individual species within the groups in terms of refugia at a later time. This hypothesis of multilayered refugia has not yet been discussed adequately by botanists. It is certainly supported by the palynological data of van der Hammen (1974, 1981), who has demonstrated clearly the occurrence of many changes in the vegetation of the Andean vegetation. It is also backed up by my own unpublished data on relationships of and within the species groups of the genus *Couepia* (Chrysobalanaceae). The multilayered effect is ob-

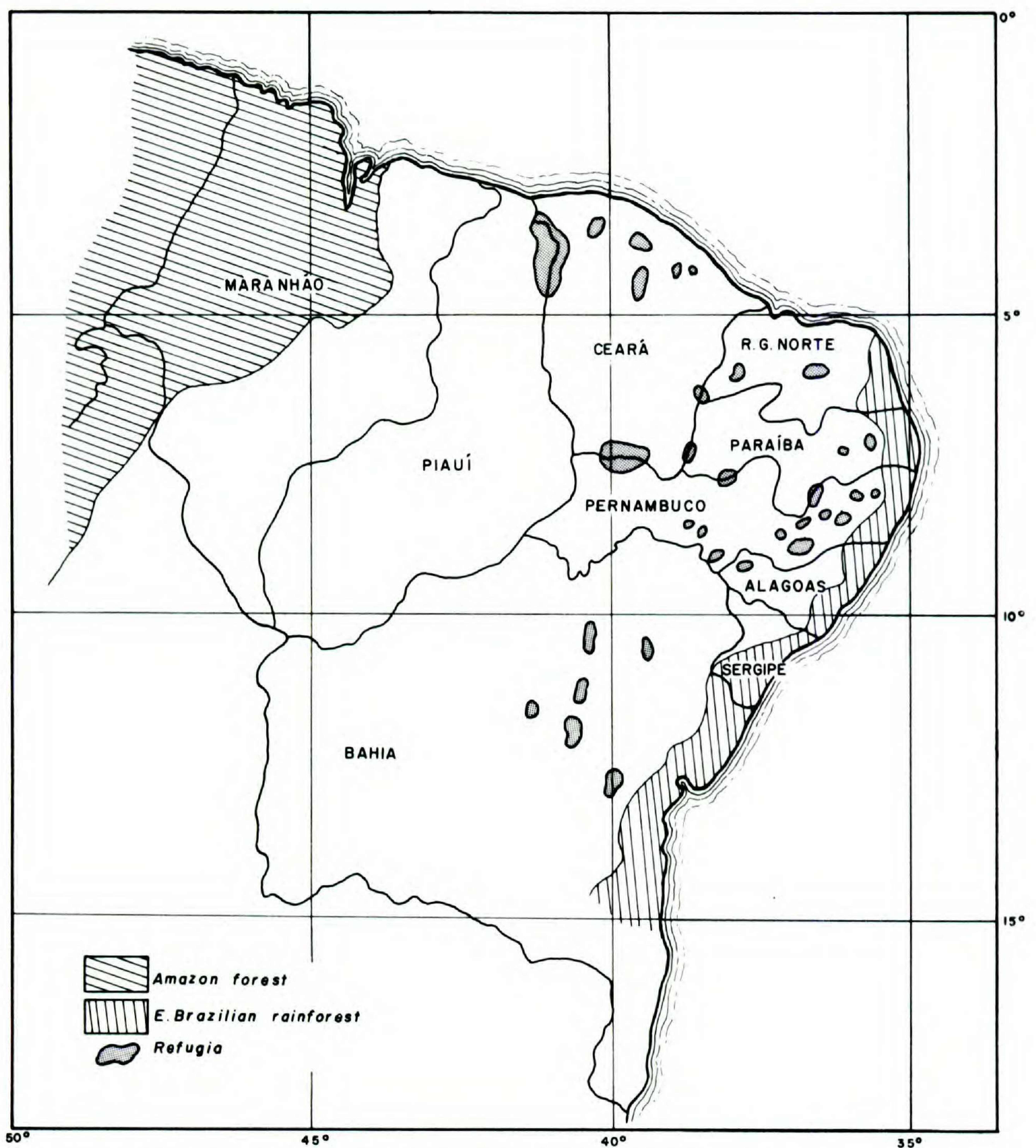


FIGURE 12. Distribution of forest refugia within the predominantly arid northeastern Brazil. Most refugia are *brejos* on low elevation mountains (after Andrade-Lima, 1981).

viously harder to discern and only patterns resulting from the later dry periods are likely to be readily discernible in present day vegetation patterns. This multiple effect of several expansions and contractions of the neotropical vegetation is obviously in need of further study by botanists.

The above review of treatment of the refuge theory by botanists shows that various authors have accepted and commented on the refuge theory, but there are still few detailed studies. Botanical evidences are based on centers of endemism and disjunct distribution and to a lesser extent on xerophytic adaptations of rain forest plants and the variation patterns in polymorphic ochlospecies. The

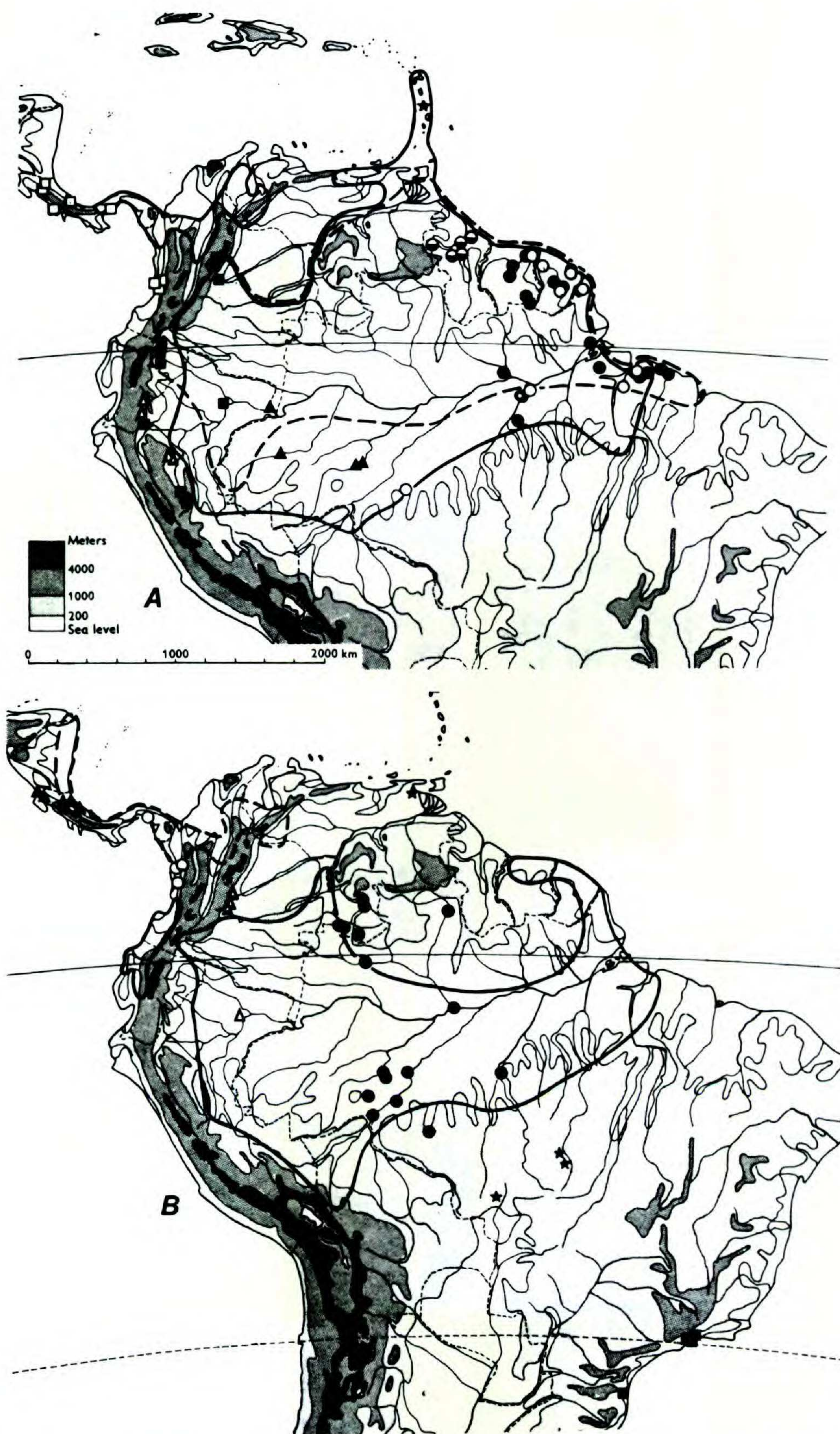


FIGURE 13. The multilayered distribution patterns of *Ischnosiphon* from Andersson (1979).

collection sample is uneven through the lowland neotropics, which also restricts the use of botanical data. However, we now have a good idea of many of the endemism centers. The highland areas are rather different from the lowlands and they offer very definite evidence of the climate changes. Further details of the

highlands are found in B. Simpson (1975, 1978) for the Andean area and in Steyermark (1979) for the Guayana Highlands.

Many of the authors cited have stressed the importance of edaphic adaptations and areas which are endemism centers of significance because of some special habitat. It is important not to confuse these with refugia, for example the white sand vegetation types. Species which are adapted to white sand usually do not occur elsewhere and are often local endemics or disjuncts because of the availability of suitable edaphic conditions. The treatment of Steyermark (1981) for Venezuela gives many examples of these edaphic endemism centers which cannot be regarded as evidence of the effect of historic climate changes on the vegetation.

Several authors cited above have mentioned polymorphic widespread species (ochlopecies in the sense of White, 1962). Examples include *Mouriri grandiflora* A. P. DC., *M. vernicosa* Naud., and *M. guianensis* Aubl. (Morley, 1975); *Licania apetala* (E. Mey.) Fritsch. (Chrysobalanaceae, cited in Prance, 1973) and *Tabebuia ochracea* (Cham.) Standl. (Gentry, 1979). These variable species are not clearly divided into subspecific taxa, yet show considerable morphological variations throughout their range. This can be both in response to present day variables and in response to previous changes. These changes should be studied further in relationship to refugia location and variability.

One of the biggest disadvantages of the methods used for delimitation of refugia in botany is that it is based on the individual taxonomist's concept of species. When centers of endemism and centers of diversity are the only criteria for the selection of refugia, then the individual species are crucial. It is hard to obtain an even species concept amongst taxonomists. This problem should certainly be considered, as evidence for refugia is often compiled based on species distributions. Some of the more sophisticated methods used by zoologists, such as hybridization zones and analysis of variation, are not so dependent upon the individual taxonomist's definition of a species.

The majority of authors cited concur that the refuge theory is likely to apply to their taxa, and have commented on part or all of the forested area of South America. Studying their distribution maps, we have a good idea of endemic centers in the South American tropical rain forest, the most important which are shown in Fig. 4. While the botanical distribution data reflect the well established changes in vegetation cover, their actual role in speciation has been less well defined. A priority for further work is a greater analysis of the speciation which occurred in the isolated refugia.

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